INTROGRESSION IN CANADIAN POPULATIONS OF *LYCOPUS AMERICANUS* MUHL. AND *L. EUROPAEUS* L. (LABIATAE)

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The genus *Lycopus* was the subject of an extensive taxonomic monograph by Henderson (1962). He recognized fourteen species, of which eight are native to North America. A ninth species, *L. europaeus* L., is naturalized in eastern North America and is now well established in a number of localities. A detailed account of the distributional history of this species was given by Stuckey and Phillips (1970), who concluded that the species is established on the eastern coast of the United States and is probably actively spreading through the Great Lakes region.

This investigation was initiated in 1971 when the second author examined a population of *Lycopus* occurring on the shore of Lake Ontario at Rattray Marsh, about 30 km west of Toronto. Although apparently consisting of only a single species, *L. europaeus,* this population showed variation in some diagnostic characters which extended beyond the range limits previously recorded for this species (Fernald, 1950; Gleason, 1952; Henderson, 1962; Ball, 1972).

A more detailed investigation was carried out by the first author in 1973 and was further expanded in 1974. At an early stage of the investigation it became apparent that the descriptions and key given by Henderson (1962) did not afford a satisfactory means of distinguishing between *Lycopus europaeus* and *L. americanus* Muhl. It was therefore necessary to make a critical reassessment of the features that can be utilized to separate these two species before any conclusions could be reached regarding the Canadian material of *L. europaeus.*

Ruttle (1932) published chromosome counts of $2n = 22$ for specimens of *Lycopus europaeus* (from Buckow, Germany) and *L. americanus* (from Kashong Glen, near Geneva, New York, U.S.A.). Several more counts for European specimens of *L. europaeus* have supported Ruttle's report (Tischler, 1934; Rohweder, 1937; Ehrenberg, 1945; Gadella and Kliphuis, 1963; Hindakova and Cincura, 1967).

MATERIALS AND METHODS

Samples of 66 specimens of *Lycopus americanus* and 53 specimens of *L. europaeus* were examined from the following herbaria (abbreviations according to Holmgren & Keuken, 1974): BM, DAO, HAM, RNG, TRT, and TRTE. The sample of *L. americanus* included specimens collected from localities where *L. europaeus* did not occur. The sample of *L. europaeus* included only European collections. The specimens were selected to cover, as far as possible, both geographical and morphological variation. Taxonomic characters and the range of variation of discriminating characters were evaluated from these two samples.

Mass collections were made from the following Canadian mixed populations of *Lycopus americanus* and *L. europaeus*: Toronto Island, York Co., Ont. (25 specimens); Rattray Marsh, Peel Co., Ont. (39 specimens); Levis, Levis Co., Que. (23 specimens); Portneuf, Portneuf Co., Que. (13 specimens); and Berthierville, Berthier Co., Que. (10 specimens). Measurements of the useful taxonomic characters, as determined from the herbarium material of *L. americanus* and of European *L. europaeus,* were recorded for the specimens from the five Canadian populations. The data were subjected to a principal components analysis. Pictorial scatter diagrams were also constructed. Specimen citations and the original data have been sent to the National Research Council of Canada, Ottawa.

In addition, smaller samples were collected from populations at the following Ontario localities: along the Grand River at Galt, Waterloo Co.; Oakville, Halton Co.; Etobicoke, York Co.; and High Park, York Co. As these samples each consisted of fewer than 10 individuals, the data from these populations was not analyzed by the methods mentioned above.

Live specimens of *Lycopus europaeus* were grown from seed obtained through seed exchange with the following European Botanic Gardens: *Austria*, Botanischer Garten und Arboretum der Stadt Lizt Danau; *France*, Jardin Botanique, Rouen; *Germany*, Gottingen, Jena, Friedrich Schiller Universitat; Munchen-Nymphenberg Botanischer Garden; *Switzerland*, Geneve, Conservatoire et Jardin Botanique. Specimens of *L. americanus* were transplanted or grown from seed gathered at localities where *L. europaeus* had not been reported. Live specimens of *Lycopus* from the Canadian mixed populations were transplanted or grown from seed. The live specimens were used to compare pollen viability and

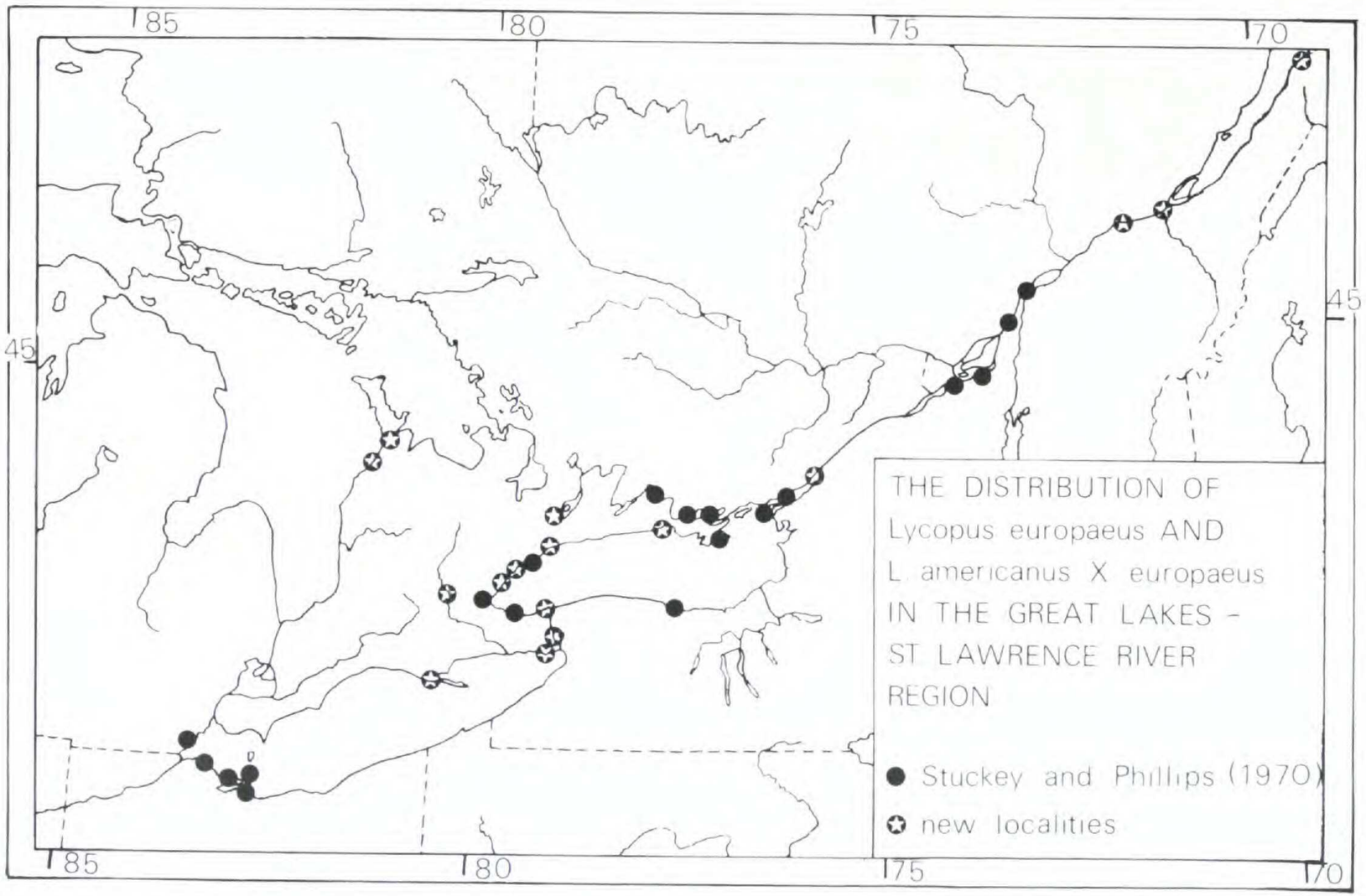


Figure 1. The distribution of *Lycopus europaeus* and *L. americanus* × *europaeus* hybrids in the Great Lakes–St. Lawrence region.

characters which proved to be difficult to observe satisfactorily on dried plant material. A few specimens were examined cytologically.

Slides of root tip and anther preparations were made according to the methods outlined by Radford *et al.* (1974; pp. 251–257). Chromosome counts for specimens of *Lycopus americanus* and *L. europaeus* were determined. Voucher specimens were deposited in the Erindale College Herbarium (TRTE).

TAXONOMIC CHARACTERS

A general review of the taxonomic characters of *Lycopus* was given by Henderson (1962). It is not intended to repeat this review but to consider in some detail the characters which distinguish *L. americanus* from *L. europaeus*. The observations made in this section were based on European specimens of *L. europaeus* and specimens of *L. americanus* collected from localities in which *L. europaeus* had not been recorded in North America.

1) **Stem habit.** Henderson (1962) defined a stolon as an underground, horizontal stem and a runner as an overground, horizontal stem. *Lycopus americanus* was said by Henderson to possess stolons. *L. europaeus* was said to have runners. Moreover, Henderson (1962) used this as an important character in his key to species. However, he stated (p. 103) that *L. americanus* may produce stolons at the first or second node which then grow downward, entering the soil at the base of the plant. In such instances the stolons of *L. americanus* are not strictly underground.

In practice, the type of horizontal stem produced is a difficult character to utilize. As many herbarium specimens are collected without the base, evaluation of this character is often impossible on herbarium material. In addition, observations of plants in the field and in cultivation suggest that horizontal stems are often not present. Both species may produce stolons and runners, although the latter were not commonly seen on specimens of *Lycopus americanus*. Furthermore, the runners of *L. europaeus* are not always strictly overground. In some instances the type of stem produced may be explained by movement of an unstable substrate.

2) **Stem Angles.** In his key to species, Henderson (1962, p. 105) included *L. americanus* with species having stems ". . . acutely 4-angled", whereas he included *L. europaeus* with species having

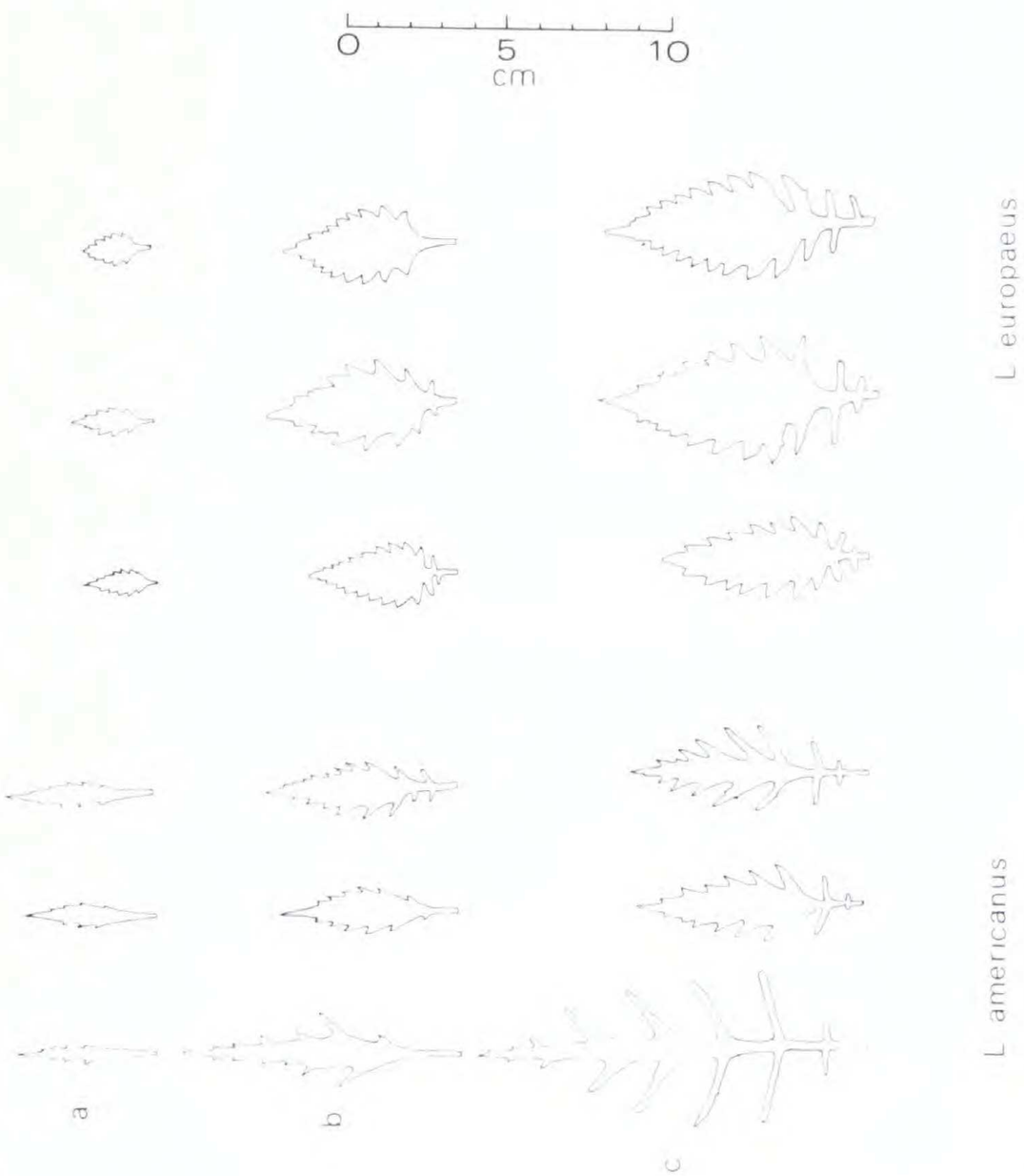


Figure 2. The shape of upper (a), middle (b), and lower (c) leaves of *Lycopus americanus* and *L. europaeus*.

stems ". . . obtusely 4-angled or rounded angles, not ridged or winged." This separation is contradicted by his description of *L. americanus,* in which he claimed that the stem angles of this species are ". . . rounded or with a prominent ridge." (p. 113).

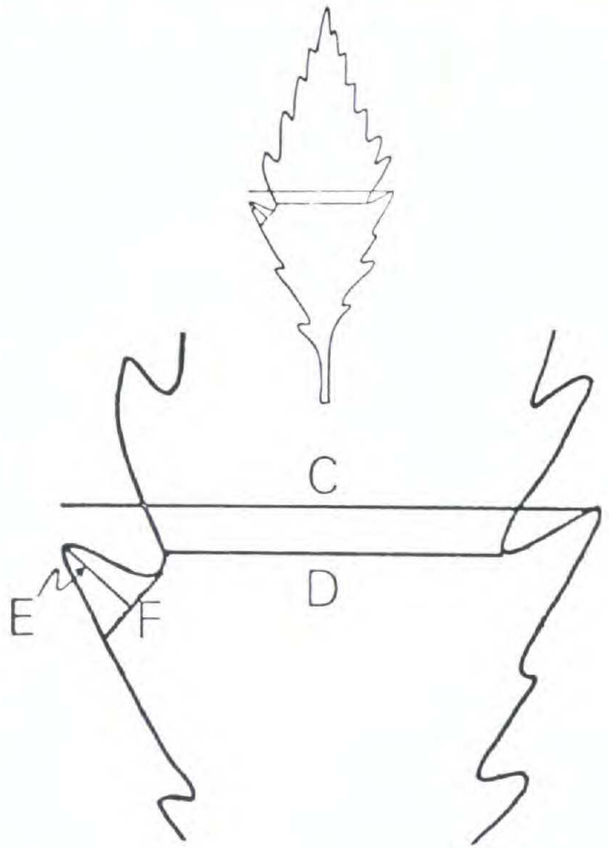
The shape of the stem angles is a difficult character to observe on dried, pressed specimens. Sections of living stems were cut from the internode below the lowest verticil. No difference in stem shape between the two species was observed. Both developed small ridges on the rounded corners of the stem to varying degrees. With increase in size, the stems lost their square shape, and rounded corners and ridges became more pronounced.

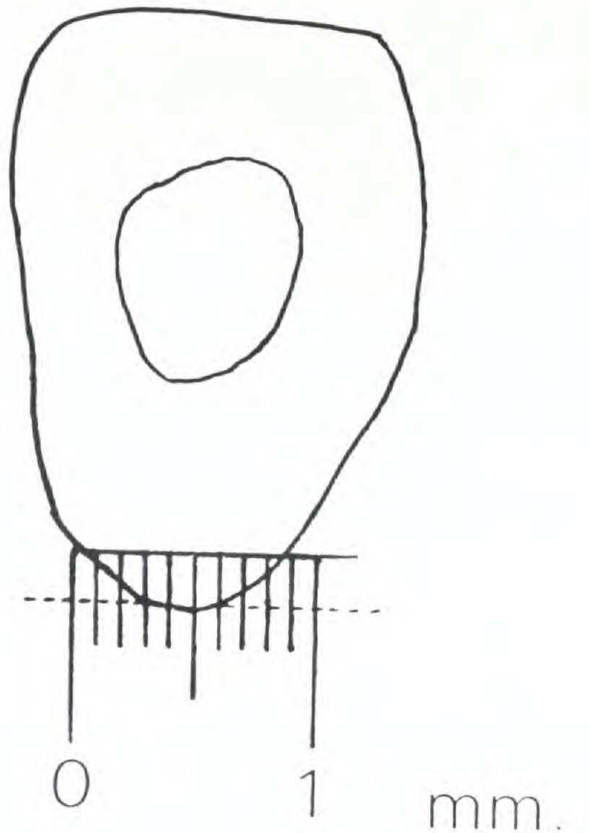
3) **Leaves.** The leaves of *Lycopus* are extremely variable. Both species have deeply lobed lower leaves and shallowly toothed upper leaves (Fig. 2). Despite this variation, the leaves do afford useful characters.

A difference in leaf shape between the species was implied by previous authors; however, these differences were not always based on comparable material. Fernald (1950) described the "lower primary leaves" of *Lycopus americanus* as ". . . lanceolate, narrowly ovate or oval . . ." and the "leaves" of *L. europaeus* as ". . . broadly lanceolate to narrowly ovate . . .". Gleason (1952) described the "leaves" of *L. americanus* as ". . . lanceolate or narrowly oblong . . ." and the "principal leaves" of *L. europaeus* as ". . . ovate or ovate-oblong . . .". Henderson (1962) described the "leaves" of *L. americanus* as ". . . linear to ovate-lanceolate . . ." and those of *L. europaeus* as ". . . ovate, ovate-lanceolate or narrowly lanceolate . . .".

In this study, leaves at the node below the lowermost verticil on the main stem were utilized. No significant differences in the leaf length or the distance from the base to the widest part of the leaf were found. The leaves of *Lycopus europaeus* were found to be significantly wider than those of *L. americanus.* However, there was considerable overlap in the ratio of leaf width divided by leaf length (Fig. 5a).

Subtle differences in the shape of the leaf teeth and the degree of lobing of the leaves were observed (Fig. 2). These characters were measured at the widest part of the leaf as shown in Fig. 3. The leaf teeth of *Lycopus europaeus* were observed to be wider and more blunt than those of *L. americanus.* This difference was quantified by the ratio EF (tooth length divided by tooth width). A histogram of





Figures 3 & 4.

3 (Left) Location of leaf measurements used in this study: **C** — maximum leaf width at widest point of the leaf, **D** — minimum leaf width at widest point of the leaf, **E** — leaf tooth length and, **F** —leaf tooth width.

4 (Right) Position of scale used to measure the width of the nutlet base and distance between the ends of the nutlet 'collar' (when present). The scale was positioned in such a way that the bottom of the nutlet was at the midpoint of the 0.1 mm division lines of the scale (here indicated by the dotted line). The width of the base of the nutlet was therefore measured about 1/4 mm above the actual base.

this character (Fig. 5b) shows that tooth shape afforded a good, but not complete, separation of the two species.

The leaves of *Lycopus americanus* were observed to be more deeply lobed than those of *L. europaeus*. The ratio CD (width of the leaf at the widest point of the leaf divided by the width between the lobes) was used to compare the degree of lobing, or division, of the leaves. As shown by the histogram (Fig. 5c), this character afforded some separation of the two species.

In his description of the species, Henderson (1962) noted that the leaf surface of *Lycopus americanus* is glandular-punctate whereas that of *L. europaeus* is closely glandular-punctate. No difference in the degree of this condition was observed in this study.

Another character which is difficult to observe on dried material is the leaf texture. Leaves of live *Lycopus europaeus* are rugose; those of *L. americanus* are smooth. As insufficient live material was examined, this character was not used in this study.

4) **Indumentum.** Little attention has been given to indumentum differences between these two species. Both species are variable in the density of the indumentum, but *Lycopus americanus* is most frequently sparsely hairy, whereas *L. europaeus* is often densely hairy. Both species may be nearly glabrous.

The full range of variation found in *Lycopus europaeus* does not appear to be present in Canada. Nothing resembling the very densely hairy plants described as *L. europaeus* subsp. *mollis* (Ball, 1972) has been found in this investigation. We therefore disagree with Fernald (1950), who claimed that this plant (which he called a variety) was present in the United States and southern Ontario. As *L. europaeus* subsp. *mollis* is restricted to the southeastern part of the range of the species, the populations found in Canada are most likely to have originated from northern or western Europe.

The substantial variation in density of indumentum found in both species has tended to obscure a difference in the nature of the hairs. Fernald (1950) possibly hinted at the difference when he described the upper surface of the lower and median primary leaves of *Lycopus europaeus* as strigose and the lower surface as slightly pubescent to glabrescent whereas the lower primary leaves of *L. americanus* were said to be glabrous or minutely pubescent on the veins beneath.

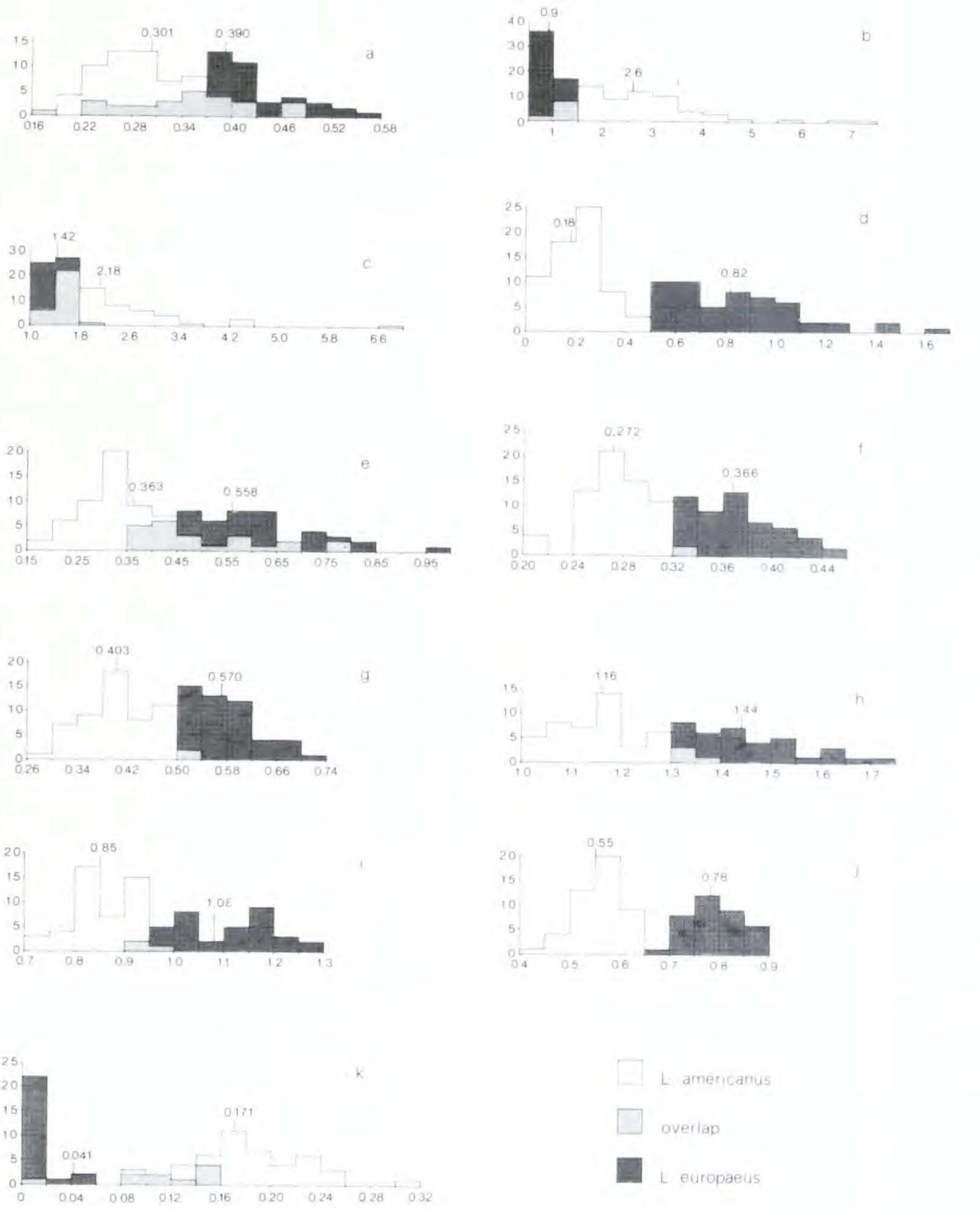


Figure 5. Histograms of characters in which *L. americanus* and European *L. europaeus* were found to differ: (a) ratio C:A — leaf width C, divided by leaf length A; (b) ratio E:F — leaf tooth length E, divided by leaf tooth width F; (c) ratio C:D — maximum leaf width C, divided by minimum leaf width D; (d) hair length in mm, (e) bracteole length in cm, (f) calyx length in cm, (g) anther length in mm, (h) nutlet length in mm, (i) nutlet width in mm, (j) width of nutlet base in mm, (k) distance between ends of nutlet collar in mm.

The difference that has been observed in this study is in the length of the hairs on the lower surface of the leaf below the lowest verticil. Measurements of hair length afforded a complete separation of the species (Fig. 5d). The hairs of *L. americanus* were 0.01–0.50 mm long whereas those of *L. europaeus* were 0.50–1.60 mm long.

5) **Bracteole Length.** The structures referred to here as bracteoles are identical with the 'inflorescence bracts' of Henderson (1962) and the 'bracts' of Gleason (1952) and Fernald (1950). The term bracteole is used here to avoid confusion with the leaves subtending the verticils, which are also sometimes referred to as bracts. Henderson (1962) reported the bracteoles of *Lycopus americanus* to be ". . . up to 3 mm long . . . at least as long as the calyx lobes of the outermost flowers . . ." and those of *L. europaeus* to be ". . . 3–5 mm long . . . slightly shorter than the calyx lobes of the outermost flowers . . .". Gleason (1952) stated that the bracteoles of *L. americanus* are ". . . about equaling the calyx . . .", whereas those of *L. europaeus* are ". . . much like *L. americanus* . . .". Fernald (1950) mentioned only that the bracteoles of *L. americanus* are "short".

In this investigation, considerable difficulty was experienced in obtaining strictly comparable material. The bracteoles were found to vary substantially, even in the same verticil. The longest bracteole of the lowest verticil was measured. Often the bracteoles are deciduous in older individuals. In such instances the longest bracteole at a higher node was measured. The mean bracteole length of *Lycopus americanus* was 3.6 mm, whereas the mean bracteole length of *L. europaeus* was 5.6 mm. Although these means are statistically different, there is considerable overlap in the measurements (Fig. 5e).

6) **Calyx and Calyx Lobe Length.** Henderson (1962) described the calyx of *Lycopus americanus* as ". . . reaching to the sinuses of the corolla . . ." and the calyx of *L. europaeus* as ". . . 2.8–3.2 mm long, almost as long as the corolla tube . . .". Henderson's (1962) failure to state the calyx or calyx lobe length for *L. americanus* is surprising, as Gleason (1952) used the length of the calyx lobes as a key character to separate the two species.

Some problems exist in utilizing this lobe length character because of the zygomorphic structure of the calyx. To avoid this problem, the overall length of the calyx, from the base to the tip of the longest lobe, was measured. Calyx measurements were taken

from the lowermost verticil of the main stem. As the calyx was observed to expand as the nutlets mature, calyces containing mature or only slightly immature nutlets were measured.

A significant difference in calyx length was found between the two species with only a minimum of overlap (Fig. 5f). The calyces of *Lycopus americanus* were found to be 0.20–0.33 cm long; those of *L. europaeus* were 0.30–0.45 cm long. The greater lengths of the calyces of *L. europaeus* are, in part, due to the comparatively longer subulate tips of the calyx lobes.

7) **Corolla.** Henderson (1962) stated that the corolla tube of *Lycopus americanus* expanded ". . . abruptly into a campanulate throat . . ." whereas that of *L. europaeus* expanded "gradually". A problem with this character arises from the tendency of the species to produce small female flowers later in the season, the corolla tubes of which expand very slightly, as well as perfect flowers which are usually produced early in the season. Only perfect flowers were compared in this study. Although a tendency of the corolla tubes of *L. americanus* to expand more abruptly than those of *L. europaeus* was observed, much overlap was found.

The corollas of both species are strikingly similar. No differences in corolla tube length, shape of the corolla lobes and pattern of purple dots at the mouth were found.

8) **Anthers.** No previously published data on the anther length of these two species has been traced. Examination of live material showed that there was a difference in anther length between the species, and that the character was not correlated with the size of the corolla tube or the position of the verticil on the plant.

As the anthers of dried specimens shrivel, care was taken to soak the anthers in a soap-water solution prior to measurement. Due to the difficulty of obtaining mature nutlets and flowers on a single specimen, anthers measured generally came from upper verticils. The longest anther lobe of a flower was measured. Anther length gave an almost complete separation of the species (Fig. 5g). The anthers of *Lycopus americanus* were 0.26–0.50 mm long, those of *L. europaeus* were 0.50–0.70 mm long.

9) **Nutlets.** The value of nutlet characters as a means of distinguishing species of Lycopus was noted by Hermann (1936). How-

ever, the nutlets of *L. europaeus* were not discussed in this article. Fernald (1950), Gleason (1952) and Henderson (1962) noted that the nutlets of *L. europaeus* are larger than those of *L. americanus*. This difference was confirmed in this study.

Nutlets of *Lycopus americanus* were 1.00–1.37 mm long, by 0.73–0.95 mm wide; those of *L. europaeus* were 1.30–1.73 mm long, by 0.93–1.25 mm wide. The variation of these characters is shown in Figs. 5h and 5i.

The shape of the base of the nutlet is a useful character which is difficult to quantify. Nutlets of *Lycopus americanus* have a narrow base, which gives them a wedge-shaped appearance. Those of *L. europaeus* have a broader base, and are comparatively more square. Comparable measurements were made by placement of a scale on the nutlet, as shown in Fig. 4. The bases of the nutlets of *L. americanus* were between 0.42 and 0.64 mm wide; those of *L. europaeus* were 0.69 and 0.80 mm wide (Fig. 5j).

The 'collar' shape, which is visible on the margins of the abaxial surface of the nutlets (cf. Fig. 6) is another useful character. The distance between the ends of the 'collar' for nutlets of *Lycopus americanus* was 0.10–0.30 mm. In comparison, the ends of the 'collar' are thicker and the resultant distance between the ends, 0–0.20 mm, was less for *L. europaeus* (Fig. 5k). The ends of the 'collar' on the nutlets of this species are confluent (cf. Fig. 6a), so that a ring, rather than a 'collar' appears.

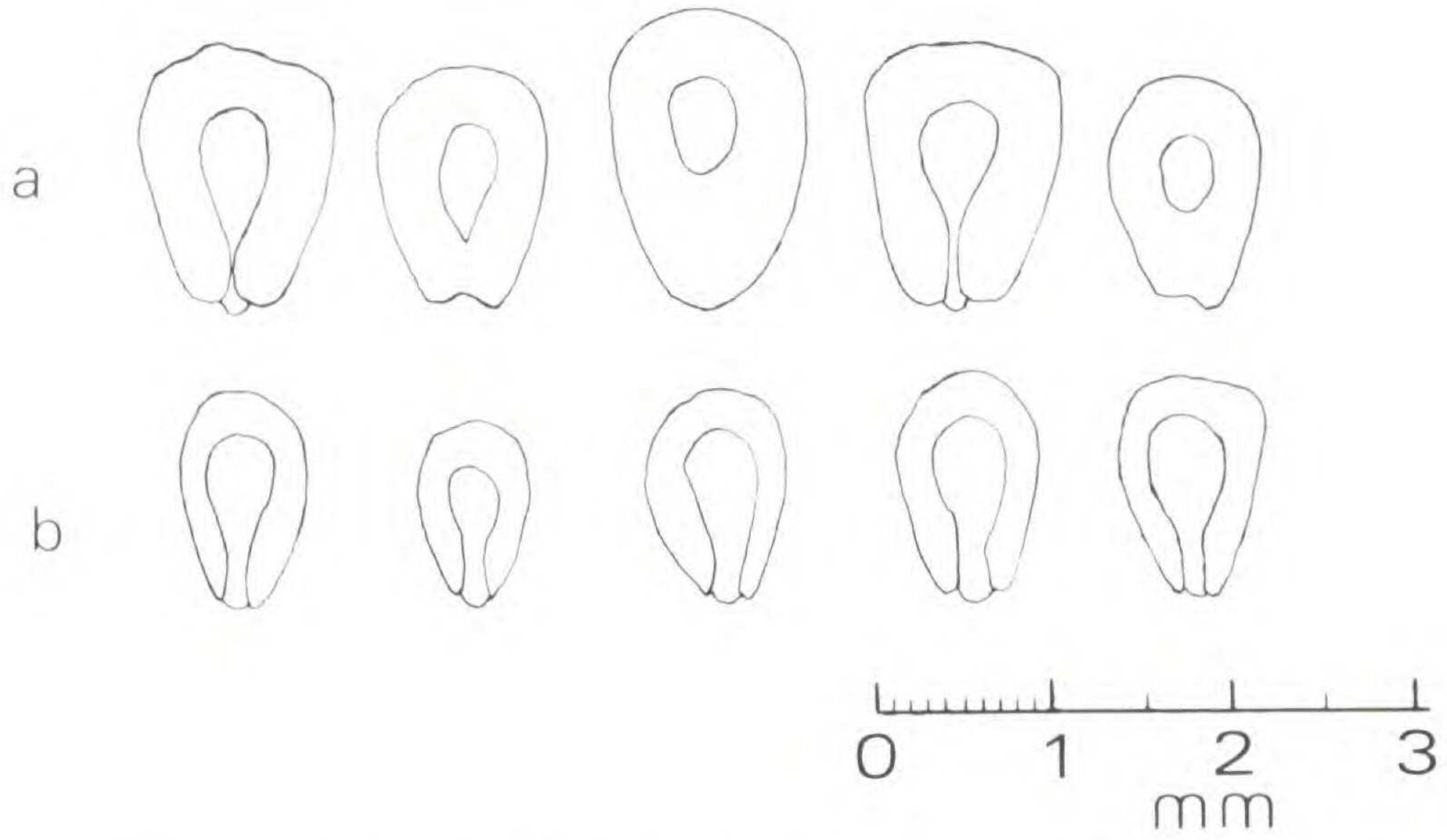


Figure 6. Shape of nutlets of *Lycopus europaeus* (a) and *L. americanus* (b).

10) **Chromosome Counts.** Despite difficulty in interpretation due to the persistence of oil droplets, the chromosome number of one specimen of *Lycopus americanus* (Erindale College Campus, Peel Co., Ont., 9 Aug., 1973, *J. Webber No. 6*) is $n = 11$. This number confirms Ruttle's (1932) count of $2n = 22$.

The chromosome number of Canadian *Lycopus europaeus* (Toronto Island, York Co., Ont., 15 Sept., 1973, *J. Webber No. 332*) is $2n = 22$. This count is identical to the number previously reported for this species from Europe, as discussed above. As the chromosome numbers of the two species are identical, chromosome number was not further utilized in this study.

CHARACTER ANALYSIS

Principal components analysis

The thirteen characters used in the principal components analysis are listed in Table 1. The principal components analysis programme contained in the NTSYS '74 programme package (Rohlf, F. J. et al. 1974) was utilized. The R technique was applied to the data matrix of 13 rows (characters) and 229 columns (specimens of *Lycopus americanus*, European *L. europaeus* and *Lycopus* from the five Canadian populations). Data was standardized before the calculation of Pearson correlation coefficients.

Table 1. **Characters used in Principal Components Analysis.**

1. leaf tooth width (cm)
2. ratio of leaf tooth length divided by leaf tooth width
3. ratio of maximum leaf width (at widest point of leaf) divided by minimum leaf width (at widest point of leaf)
4. leaf hair length (mm)
5. bracteole length (cm)
6. calyx length (cm)
7. anther length (mm)
8. nutlet length (mm)
9. nutlet width (mm)
10. nutlet base width (mm)
11. distance between ends of nutlet 'collar' (mm)
12. maximum leaf width (cm)
13. leaf length (cm)

Eight principal components were extracted. Components 1, 2 and 3 accounted for 48.47%, 15.17% and 7.87% of the trace, respectively. Subsequent principal components accounted for smaller percentages of the trace. The steep drop in variance of the first, second and third principal components is in keeping with analyses which show good separation of groups (Blackith & Reyment, 1971).

As the first principal component accounts for nearly half of the variance, the best separation was expected to be shown by this axis. This expectation is confirmed by examination of the projection of the first and second principal components (Fig. 7). This projection shows that *Lycopus americanus* is completely separated from *L. europaeus* on the first axis. The majority of the individuals from the Canadian populations are intermediate between *L. americanus* and *L. europaeus,* although some individuals fall into the ranges of the clusters of the parent species. The intermediates tend to resemble *L. europaeus* more than *L. americanus.*

Pictorial Scatter Diagrams

Pictorial scatter diagrams were constructed following the techniques of Anderson (1949). Five characters which showed the greatest separation between *Lycopus americanus* and *L. europaeus* were chosen. Two of these characters were used as the axes. The three remaining characters were scored, symbolized, and added to the appropriate points of the scatter diagrams. Data from Canadian populations of *Lycopus* were similarly analyzed and compared with the data from specimens of *L. americanus* and *L. europaeus* (Fig. 8). Unlike the principal components analysis, specimens with missing characters could not be included in the pictorial scatter diagrams. Therefore, many specimens from the Canadian populations are excluded from the pictorial scatter diagrams.

The results obtained by applying conventional Andersonian techniques to the data agree with the findings of the principal components analysis. As shown by Fig. 8, the majority of the individuals from the Canadian populations are intermediate between *Lycopus americanus* and *L. europaeus,* although some individuals fall within the clusters of the parent species. The intermediates tend to resemble *L. europaeus* more than *L. americanus.*

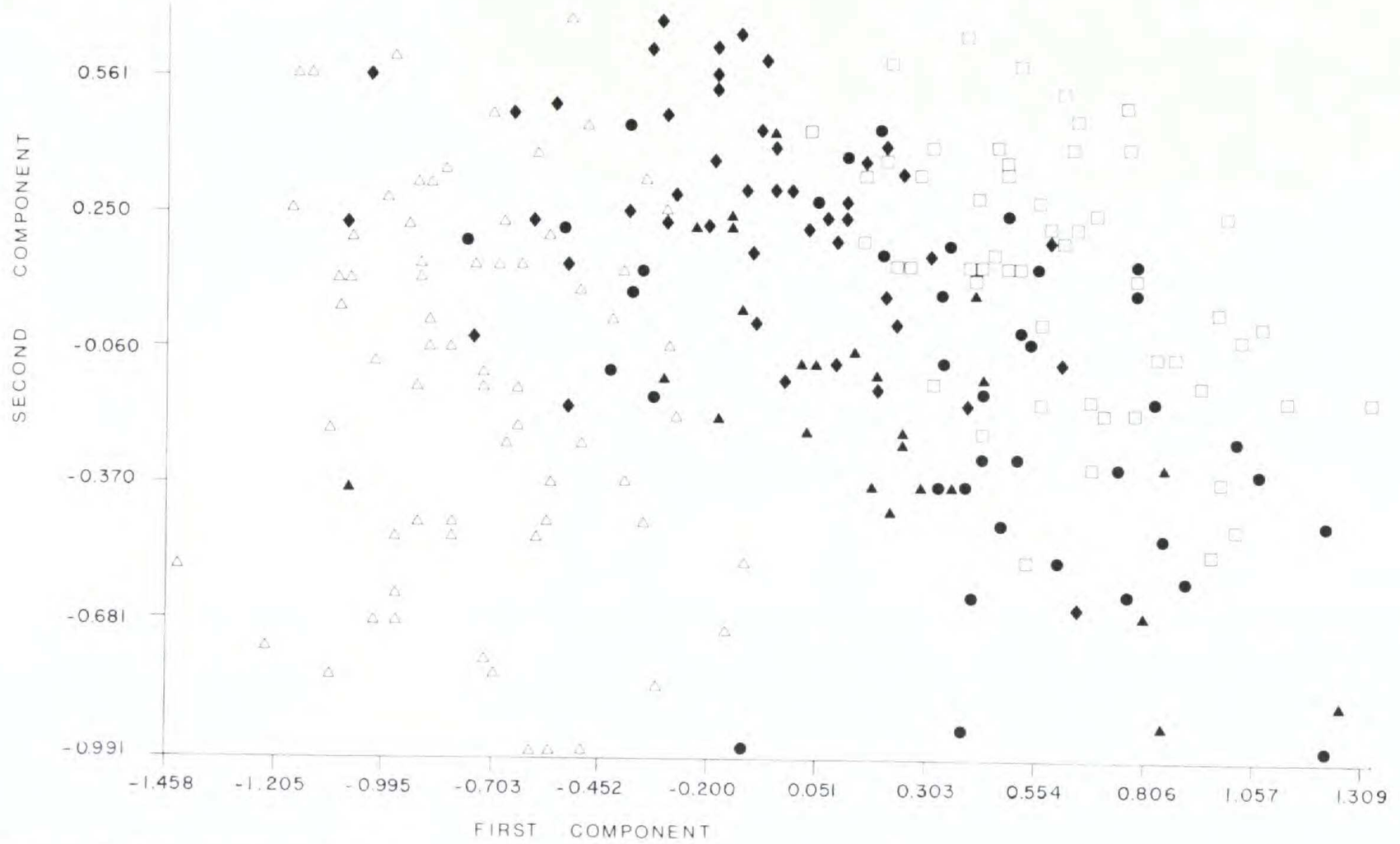


Figure 7. Bivariate plot of specimen scores on the first and second principal components: △ *L. americanus* (collected from areas in Ontario and Quebec where *L. europaeus* had not been reported); □ *L. europaeus* (collected from Europe); ● specimens of Lycopus from Rattray Marsh; ▲ specimens of *Lycopus* from Toronto Island; ◆ specimens of *Lycopus* from Quebec populations.

ANALYSIS OF CANADIAN POPULATIONS OF LYCOPUS

In most cases the sample sizes gathered from five localities in Ontario and Quebec were small. Although there was often apparently a large number of individuals, many of these were found to be clones and therefore only one part of the clone was taken. As mentioned previously, difficulty in obtaining specimens with both fruit and anther characters was a problem.

All of the Canadian populations examined contained individuals with principal component scores (in the case of principal components analysis) or combinations of characters (in the case of pictorial scatter diagrams) which extend beyond the ranges for *Lycopus americanus* and *L. europaeus*. All populations contained at least one individual with principal component scores within the range for *L. europaeus*. Specimens resembling *L. americanus* were much less frequent, although at least one individual of this species was found in each population. The intermediate nature of many specimens is also shown by both the principal components analysis (Fig. 7) and the pictorial scatter diagrams (Fig. 8). The populations examined from Ontario and Quebec are discussed as follows:

Toronto Island population

Lycopus europaeus was first collected from Toronto Island in 1903 (*Scott*, TRT), and appears to have become established. The species now occurs scattered over most of the shoreline. Seedlings readily become established in lawns which are inundated in the spring. *L. americanus* is present in the same habitats, although it is not nearly so common. The population sampled was a patch on 0.1 hectare, 20 m west of the Island School.

Although both *Lycopus americanus* and *L. europaeus* occurred in this population, the majority of the individuals showed combinations of characters which place them intermediate between the two species. For example, most individuals had nutlets not more than 1.30 mm long (a *L. americanus* character), whereas the leaf hairs of these individuals were generally more than 0.40 mm long (a *L. europaeus* character). In general appearance, especially in the shape and division of the leaves, most specimens resembled *L. europaeus*, and for this reason they generally have been uncritically determined as that species. This determination is contradicted by an examination of smaller, less obvious characters.

Rattray Marsh populations

This population occupied a comparatively small area. There is a strong possibility that the population originated from only a few individuals with extensive vegetative reproduction accounting for much of the spread through the locality. The first record of *Lycopus europaeus* from this locality appears to be 1959 (*A.F. Coventry*, TRTE). However, little significance can be attached to this date, there being no record of any plant collections made there prior to the late 1950's (Macdonald, 1970), although the area may have been visited by naturalists in the early 1900's (Faull, 1913).

As with the Toronto Island population, a small number of individuals fell within the ranges of *L. americanus* and *L. europaeus*, whereas the majority appeared to be intermediates.

Other Ontario populations

The remaining Ontario populations of *Lycopus europaeus* examined were restricted to marshes and riverbanks close to the shoreline of Lake Ontario. One notable exception was a population of *L. europaeus* occurring inland along the banks of the Grand River at Galt (Waterloo Co.). The sample from this locality, like the samples from High Park (York Co.), Etobicoke Creek (Peel Co.), Port Credit (Peel Co.) and Oakville Creek (Halton Co.), consisted of fewer than 14 individuals. Despite the small size of these populations, analysis by Andersonian techniques showed that these populations are similar in structure to those analyzed by principal components analysis.

Quebec populations

All localities where samples of *Lycopus europaeus* were gathered in Quebec occurred within the geographical range of *L. laurentianus* Rolland-Germain (1945), which had been collected at only a few localities along the St. Lawrence River. This species is distinguished from *L. americanus* and *L. europaeus* by the presence of conspicuous wings along the stem angles. As none of the specimens collected had winged stem angles, it was assumed that the populations sampled contained only plants of *L. europaeus* and *L. americanus*.

As shown by the principal components analysis (Fig. 7) and pictorial scatter diagrams (Fig. 8), the population samples from Levis, Portneuf, and Berthierville were similar to the Toronto Island

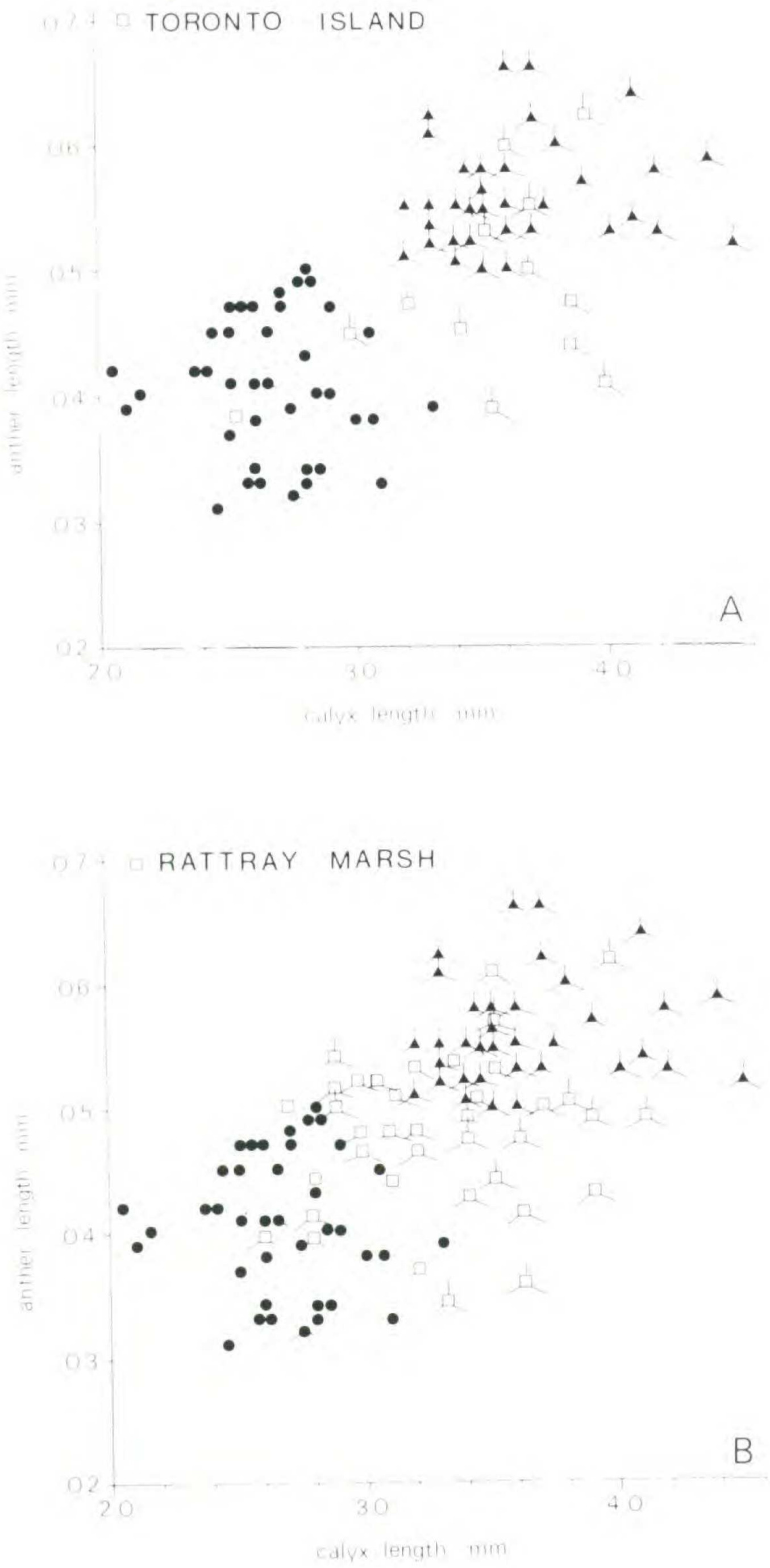
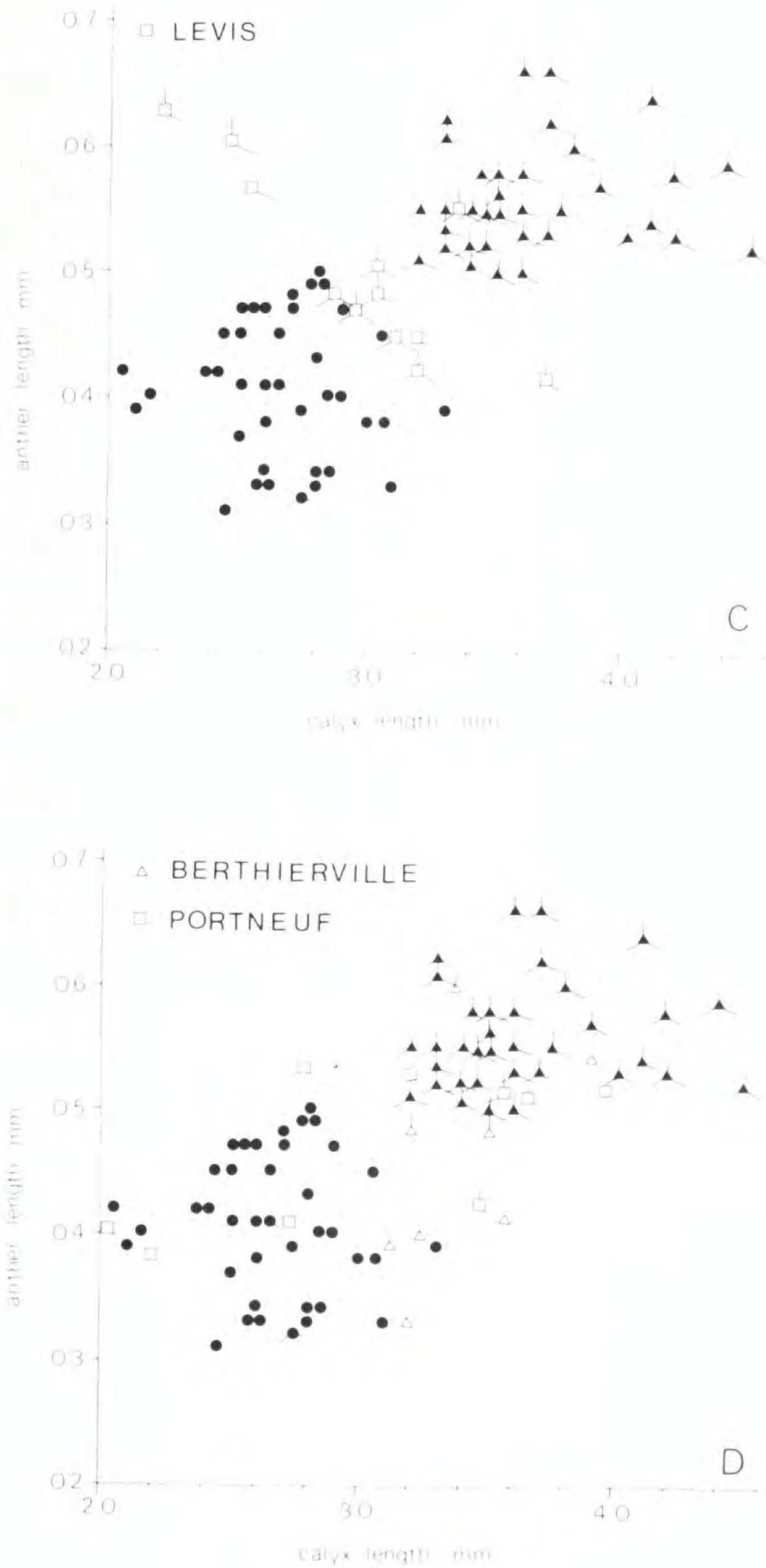


Figure 8. Pictorial Scatter diagrams of samples of *L. americanus* collected from areas where *L. europaeus* is absent and samples of European *L. europaeus* compared



with individuals from *Lycopus* populations at (A) Toronto Island, (B) Rattray Marsh, (C) Levis and (D) Portneuf and Berthierville. (see page 300 for legend)

Legend for Figure 8.

L. europaeus ▲

L. americanus ●

Hair length in mm

♂	♂	♀
≥0.50	<0.50 >0.40	≤0.40

Nutlet width in mm

♀	♀	♀
≥0.96	<0.96 >0.92	≤0.92

Nutlet length in mm

♀	♀	♀
≥1.35	<1.35 >1.30	≤1.30

and Rattray Marsh samples. A few specimens of *Lycopus americanus* were observed, as well as specimens which resembled *L. europaeus*. The majority of the intermediate specimens resembled *L. europaeus* more than *L. americanus*.

ADDITIONAL EVIDENCE

Besides the above analysis of morphological characters, the effective fertility of *Lycopus europaeus, L. americanus* and intermediate individuals was investigated as an aid to understanding the nature of the Canadian populations. The pollen of all three taxa appeared to be identical in size and shape, and staining with methylene blue indicated a high level (more than 90%) of pollen viability in all specimens examined. Fruit characters were used extensively in this study, but no evidence of sterility was detected in any specimen that was examined. All evidence indicates that the intermediate plants show no reduction in effective fertility compared with *L. europaeus* and *L. americanus*.

DISCUSSION

The results indicate that the plants named *Lycopus europaeus* in Canada are hybrid swarms derived from *L. europaeus* and *L. americanus*. In most cases, the populations examined contained a few individuals that can be referred to *L. europaeus*. Specimens of *L. americanus* were not so common in the populations examined. Usually the majority of individuals were variously intermediate between these two species with the intermediate individuals showing no reduction in effective fertility compared with *L. europaeus* and *L. americanus*. Although many known examples of the formation and

establishment of hybrid swarms are in disturbed habitats, this particular example is noteworthy as it involves a native North American species hybridizing with a European species, apparently enabling the latter to spread more rapidly into eastern Canada.

Lycopus europeaus and *L. americanus* × *europaeus* hybrids have been spreading rapidly in the Great Lakes–St. Lawrence region of Canada in recent years. They occur frequently along the shores of the St. Lawrence River and along the north-western shore of Lake Ontario. They are much less frequent along the north shore of Lake Erie and appear to have only recently spread into this area. For example, no specimens were observed at Long Point (Norfolk Co.) in 1974, but in 1975 there were many individuals on landfill sites by the marinas. Two recent records from the Bruce Peninsula in Lake Huron (*Bezdek & McAskie, 1975,* TRTE; *Johnson, 1976,* HAM), one of the few areas in Ontario frequently visited by botanists, indicate that the plants have recently spread into this lake. Collections are also known from two inland localities, Port Perry, Ontario Co. (*Leadbeater et al., 1973,* TRT) and Galt, Waterloo Co. (*Campbell, 1970*; *Webber, 1974,* TRTE), but the spread inland seems to be much slower than along the shores of the Great Lakes.

The recent establishment and spread of the hybrid swarms of *Lycopus americanus* × *europaeus* in the Great Lakes-St. Lawrence region cannot readily be explained. *L. europaeus* has been well established in a few localities, such as Toronto Island, for at least 70 years, but showed little tendency to spread from there. The recent rapid spread along the St. Lawrence River appears to have started soon after the opening of the St. Lawrence Seaway in 1955 and it could be attributed to the invasion of new stocks of *L. europaeus* directly from Europe into the St. Lawrence and Great Lakes.

It is not clear whether there have been a large number of independent invasions of *Lycopus europaeus* from Europe or whether the established populations have been the source of the spread. Many of the populations examined contain at least a few individuals that can be identified as *L. europaeus* so that the hypothesis of frequent invasion from Europe is a possibility. On the other hand, it seems more likely that there have been few invasions from Europe and that the spread through the Great Lakes–St. Lawrence region has been derived mainly from established local populations.

The plants which are now established show many of the attributes of a good colonizing species (cf. Baker & Stebbins, 1965). They are

perennials capable of extensive vegetative reproduction, and also capable of growing in and stabilizing disturbed soil and sand, and even gravel and shingle. They show a high degree of phenotypic plasticity. Small individuals, flowering when no more than 5 cm high, have been observed growing in cracks and crevices in rocks and concrete and between wooden boards of docks in many places. In sheltered, more shaded and moist areas, much branched individuals over 2 m tall have been seen. These facts, together with the high level of fertility that has been observed, could explain the success of the hybrid swarms.

The fluctuations in water level in the Great Lakes may also have assisted in the spread of these plants. This phenomenon, together with a considerable increase in human activity, has created a great many more disturbed sites along the shores in recent years.

Although it has not been possible to determine the extent to which hybridization has been an essential component in the success of these plants, the fact that all the populations examined contain a high proportion of intermediate individuals makes it clear that hybridization is undoubtedly important to the success of these plants.

Possible factors which may have contributed to the success of the hybrids (as compared to *Lycopus europaeus*) are: (**1**) increased phenotypic plasticity, (**2**) increase in the production of stolons as well as runners, and (**3**) improved adaptation to the climate of eastern North America. Only extensive comparative cultivation experiments are likely to determine which factors are the most significant.

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